

Population and community dynamics in the soil ecosystem

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SUMMARY

- 1 The review concentrates on the soil arthropods (predominantly mites and springtails) and on the effects of the environment on their population dynamics.
- 2 Among the many environmental factors which influence the fecundity, speed of development and mortality of the soil fauna, the species of organisms available for food, as well as their nutritional status, are important in determining such demographic parameters. Egg diapause, and the possibility of an egg bank in the soil, could also have important implications for year-to-year fluctuations in population density.
- 3 Competition between soil arthropods is generally asymmetrical (one species adversely affected, the other species unaffected). Predation probably plays an important role in regulating populations of the grazing species. Little is yet understood about more complex interactions in the soil ecosystem.
- 4 Succession is generally related to an increase in both the number of species and the density of most groups of the soil fauna. However, management effects are linked directly to modification of the physical habitat and to change in the soil organic matter content. The potential for perturbation experiments, replicated and designed to investigate interactions, is discussed.

INTRODUCTION

As the title of this review is wide, it is appropriate to focus particular attention on some aspects of population and community dynamics. Two restrictions will be made. First, the effect of the environment on the populations of soil animals will be reviewed. The word 'environment' in this context is defined as widely as possible, and includes all aspects of the physical, chemical and biological environments in which the soil fauna are living. However, which environmental factors influence the population dynamics, as opposed to the distribution, of the soil animals? The review is very largely concerned with the dynamic rather than the distributional aspects of soil communities: the latter have been reviewed by Usher (1976). Second, examples illustrating the review will be chosen from soil arthropod communities. These are comprised of some insects, mostly of the order Collembola (springtails), and all of the soil mites (Acari: especially Cryptostigmata, Mesostigmata and Prostigmata).

The review follows relatively traditional lines by examining three levels in the hierarchy of complexity of interactions in the soil environment. The first level is

concerned with the dynamics of single species populations, and contains an analysis of the factors contributing to population increase or decline. Simple community types, of only two or three species, the subject of laboratory experimentation, are considered in the second level. Naturally occurring communities are looked at in the third level. The aim of the review is, therefore, to investigate the factors determining the sizes of the individual species populations, and the way in which these interact to form the community of soil animals. The review thus differs from two previous reviews on similar topics (Usher *et al.* 1979; Usher, Booth & Sparkes 1982).

DYNAMICS OF SINGLE SPECIES POPULATIONS

The basic equation in population dynamics is

$$N_{t+1} = N_t + B - D + I - E$$

where N is the number of animals, B and D are the number being born and dying respectively in the time period t to $t + 1$, and I and E are the numbers of immigrants and emigrants during the same period. Various facets of this equation will be considered in the review, which will not be concerned with the methodology of parameter estimation from field data (cf. Straalen 1983b) or with the prediction of final population densities (cf. Sager & Stelter 1981). Relatively little is known about the demography of soil animal populations, as evidenced by the final plea in Joosse's (1983) review of Collembolan ecophysiology.

Fecundity

A number of species, particularly those associated with more stable environments, breed only once (Huhta & Mikkonen 1982; Leinass & Bleken 1983) or twice (Grégoire-Wibo 1979) per year. The capacity for increase can be small: a value of $r = 0.00008$ per degree-week was estimated for *Ceratozetes kananaskis* by Mitchell (1977). However, in less stable environments, more generations are likely to occur: Hutson (1981) showed that all *Collembola* colonizing reclaimed land in Northumberland had at least two generations per year and *Isotoma notabilis* reproduced continuously throughout the year.

Sexual breeding has generally been assumed. However, Petersen (1978) has shown that about 25% of species of *Collembola* in a beechwood breed parthenogenetically: these species are generally the most abundant since they comprise 72% of all individuals. *Folsomia candida* has frequently been used in laboratory studies because it is parthenogenetic. Arrhenotoky (haploid male, diploid female) is probably not uncommon in the Mesostigmata, and, with overlapping generations and without cannibalism or oophagy, Usher & Davis (1983) have suggested that at least one soil mite, *Hypoaspis aculeifer*, may be approaching the eusocial threshold.

Before eggs are laid it has been suggested that a protein-rich meal is required

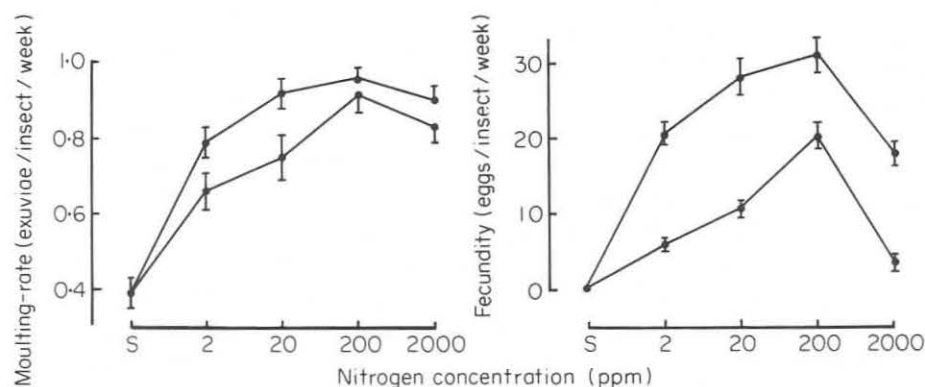


FIG. 1. The rate of development, measured as the moulting rate, and the fecundity of *Folsomia candida* when starved or feeding on two species of fungi, *Hypholoma fasciculare* (upper graphs) and *Coriolus versicolor* (lower graphs), which had been cultured in media with a variety of nitrogen concentrations. Vertical bars indicate ± 1 standard error. Data from Booth (1979).

(pollen feeding by *Entomobrya socia*, Waldorf 1981), or that methionine is essential (required by *Achipteria holomensis*, Stamou *et al.* 1981). A 6-year study of a population of *Allodinychus flagelliger* by Athias-Bincé (1978/79) indicated that fecundity was strongly density-dependent. Webb & Elmes (1979) showed that the number of eggs and pre-larvae of *Steganacarus magnus* was closely correlated with female size, and Grimnes & Snider (1981) showed that four electrophoretically distinct strains of the parthenogenetic *F. candida* have different fecundities. However, in an interesting study that related fecundity to food quality, Booth (1979) grew two species of fungus in liquid media with 2, 20, 200, and 2000 ppm of nitrogen, and determined the fecundity of *F. candida* when fed with these eight types of food (see Fig. 1). It is clear that fecundity was greater when *F. candida* was feeding on *Hypholoma fasciculare* than on *Coriolus versicolor*, and that fecundity increased with increasing nitrogen content up to 200 ppm. The critical experiment that Booth (1979) performed was to see if *F. candida* preferred the food that optimized fecundity. This was the case when *F. candida* were feeding on the less preferred fungus (Table 1), but there was no such relationship with the preferred

TABLE 1. The mean number of *Folsomia candida* observed feeding on fungi grown in media with different nitrogen concentrations. The data are taken from two experiments performed by Booth (1979), one experiment using *Coriolus versicolor* and the other *Hypholoma fasciculare*. Standard errors (SE) and least significant differences (LSD) are based on the analyses of variance of the data of each experiment.

Nitrogen concentration (ppm)	<i>C. versicolor</i>	<i>H. fasciculare</i>
2	6.4	4.4
20	4.6	1.4
200	9.4	2.0
2000	5.1	3.8
SE of means	1.0	0.8
LSD (at 5% level)	3.0	2.2

fungus. The extent to which both food type and food quality affect fecundity in field populations remains unknown.

It is possible that the eggs may go into diapause. In northern Europe, egg diapause by *Lepidocyrtus lignorum* is terminated after cold treatment so that there is synchronous hatching in the spring (Leinaas & Bleken 1983), and Valpas (1969) showed that hatching of eggs occurred whilst samples, particularly those that were frozen or water-logged, were being extracted in the laboratory. Some eggs of *Sphaeridia pumilis* diapause, whilst others, particularly those laid in autumn, did not (Blancquaert, Mertens & Coessens 1982). This leads to speculation that the soil may contain an 'egg bank' of arthropod eggs in much the same way as it contains a 'seed bank' of higher plant seeds. Studies of the Antarctic mite *Gamasellus racovitzai* (Usher & Bowring 1984) suggest the possibility of an egg bank, which is also indicated by Healey (1965) who says that 'recruitment of newly hatched individuals [of *Onychiurus procampatus*] occurs at all times'. He discusses some January samples which were frozen and appeared like blocks of ice: on extraction there were juveniles, but whether these had been present in the samples as juveniles or as eggs that hatched during extraction is uncertain. Valpas' (1969) finding of hatching during extraction is clearly important in understanding the dynamics of the egg bank in the soil. In turn, an egg bank would be important in population or community dynamics since it could release pulses of animals if there was synchronous hatching after unusual events, such as late summer rains in the Mediterranean region (Blancquaert *et al.* 1982).

Speed of development

One would expect the speed of development to be closely related to temperature. Grégoire-Wibo's (1979) field study of *Folsomia quadrioculata* phenology showed that development of different cohorts, e.g. those overwintering or those hatching from eggs in the spring, was temperature-dependent. Hutson's (1978) laboratory studies of *Folsomia candida* are similar, as development from hatching to the age of first oviposition was 6 days at 25°C, 14 days at 10°C and 85 days at 5°C. The utility of a physiological scale for measuring development time is shown by Mitchell's (1977) study of development of *Ceratozetes kananaskis* which required 465 degree-weeks (approximately 2 years at field temperatures), though this assumes linearity which is not shown in Hutson's (1978) study quoted above.

There are, however, other factors which would appear to over-ride the effect of temperature. These include the effects of water (Verhoef & Selm 1983), drought (Takeda 1983), substrate (Booth 1983), and the availability of a protein-rich food, usually pollen (Allman & Zettel 1983). The fungi being grazed can also be important. Stefaniak & Seniczak (1981) attempted to culture *Oppia nitens* on twelve species of fungi. Three species remained uneaten, the mites dying without ovipositing. The rate of ingestion of three other fungi was low, and juveniles took an average of 32.7 days to develop into adults. The ingestion rate of four fungi was high, and juveniles had a greater survival and developed into adults in an average of

30.3 days. With the two other species, which were very highly ingested, large numbers of eggs were laid, juvenile survival was high, and development averaged 26.5 days. Booth's (1979) study also showed that the speed of development, measured by the rate of production of exuviae, was greater with *Folsomia candida* feeding on *Hypholoma* than on *Coriolus* (Fig. 1). The choice experiments (Table 1) could not indicate whether *F. candida* selected the form of *Coriolus* that maximized development rate or fecundity, since the reaction to both was similar: selection of *Hypholoma* was not consistent with such optimization.

Mortality

There are two types of mortality: continuous mortality and mortality associated with a particularly harsh season of the year. The latter, usually summer heat associated with desiccation or winter cold associated with freezing, can have important consequences for the dynamics of populations. Baker (1978) has described the biology of the Australian millipede, *Ommatoiulus moreletii*, in which summer mortality can be high in populations aestivating in grasslands whereas it is negligible in woodland populations. Joosse (1983) reviewed cold adaptation in the Collembola and illustrated Burn's (1982) data for *Cryptopygus antarcticus* in which population mortality is approximately proportional to the number of insects with gut contents.

There are relatively few data on continuous mortality. Mitchell (1977) illustrated a survivorship curve for *Ceratozetes kananaskis*, which showed an exponential decay in mortality rate during the development from egg to adult. Straalen (1983a) considered methods of estimating mortality rates for populations of Collembola: the rates varied between 0.7 and 0.50 per week for *Orchesella cincta* and between 0.19 and 0.41 per week for *Tomocerus minor*. Athias-Binche (1978/79), after a 6-year study of a population of *Allodinychus flagelliger*, concluded that mortality was density-dependent. Massive mortalities (greater than 50% in less than one day) have been recorded for *Onychiurus justus* by Snider & Butcher (1973) in environments with relative humidities below 100%. The experiments of Stefaniak & Seniczak (1981) also indicated that mortality is dependent on the type of food available to the soil fauna.

However, the question which appears never to have been addressed is how the various forms of mortality can be apportioned in field populations. What proportion is due to environmental extremes, what proportion to predators, what proportion to unavailability of appropriate food, and what proportion to other causes?

Immigration and emigration

There are few data on the speed of movement of the soil fauna. Berthet (1964) marked mites radioactively, and recorded their wanderings over the subsequent few weeks: he found that the rate of daily displacement was small. In the Netherlands, studies monitoring the spread of arthropod species into newly created pol-

ders (e.g. Haeck, Hengeveld & Turin 1980), indicated a reasonably fast colonization, though this was not always due to movement within the soil or litter.

Studies of individual species have tended to indicate little movement. Petersen's (1978) study of *Tullbergia macrochaeta* in Jutland indicated that there was little mixing of a population of sexual forms (extending to at least 36 m from the seashore) and a population of parthenogenetic forms (occurring more than 50 m from the shore). Allmen & Zettel (1982) documented the vertical movement of a population of *Entomobrya nivalis* on trees: females descend to the litter to oviposit, and juveniles ascend to feed. A second migration occurs at the beginning of winter when the majority migrate down to hibernate under loose flakes of bark.

However, it remains uncertain in what way many of the species of soil animals are distributed. The wide geographical distribution of many species, contrasted with the extremely localized distributions of cave species, tends to imply efficient dispersal. Studies of colonization of new habitats, e.g. Hutson & Luff (1978) and Hutson (1981), indicate that some species arrive relatively quickly, but the number of species which arrive and fail to establish themselves is unknown. Wind dispersal (see Macfadyen in Hale 1963) is probably important, but there are no quantitative data on numbers of species or the number of individuals distributed in this way. For some species of Mesostigmata, phoresy is probably an alternative method of dispersal. Research into the methods and speed of dispersal would have interest both for the dynamics of populations and communities and for the biogeography of the soil fauna.

DYNAMICS OF COMMUNITIES OF TWO OR THREE SPECIES

Usher *et al.* (1979) reviewed the population dynamics of soil arthropods, concentrating on two approaches, termed 'divisive' (whereby inferences are made from sampling field communities) and 'agglomerative' (the inferences being drawn from putting together simple communities in the laboratory). No such approach was taken by either Usher, Booth & Sparkes (1982) or Parkinson (1983), both of whom selected a variety of topics of interest to them. In this section of the review a different approach will be taken: the three most frequent interactions—interspecific competition, predator–prey, herbivore–plant—will each be considered, and then there will be a brief review of interactions involving three trophic levels.

Interspecific competition

Competition has frequently been inferred in soil arthropod communities, but has less frequently been demonstrated. Greenslade & Greenslade (1980) suggested that diffuse competition (in which any one species interacts with a patchwork of others at varying densities and in varying combinations) occurred in a community of Isotomid Collembola from the Solomon Islands, as did Kaczmarek (1975) for a pine forest community of Collembola in Poland. Vegter (1983), however, demonstrated that a field population of *Orchesella cincta* and *Tomocerus minor*, in the

TABLE 2. A summary of the competitive interactions between *Onychiurus ambulans* and *Isotoma viridis* (Sparkes 1982). In the table results are given in the form x/y , where x represents the effect of *O. ambulans* on the survival of *I. viridis*, and y the effect of *I. viridis* on the survival of *O. ambulans*. O indicates no significant effect, and – a significant depression in survival

Initial percentage abundance of		Temperature		
<i>O. ambulans</i>	<i>I. viridis</i>	16°C constant	8°C constant	8°C mean
67	33	–/–	0/0	0/0
50	50	0/–	0/–	0/0
33	67	0/–	–/–	0/0

presence of three other species of Entomobryid Collembola, tended to avoid competition by food and microhabitat specialization. Can either competition or avoidance of competition be demonstrated in the laboratory?

Competition between two Collembola, *Isotoma viridis* and *Onychiurus ambulans*, from the community in an abandoned chalk quarry in the Yorkshire Wolds, has been investigated by Sparkes (1982). The species were cultured, either individually or mixed in varying proportions, at 8°C, 16°C, and at an average of 8°C but varying diurnally from 4°C to 12°C. At this variable temperature neither species affected the other significantly (Table 2). At constant temperature three results showed a one-way interaction (*O. ambulans* survival being depressed by the presence of *I. viridis*), and two showed genuine competition whereby the survival of both species was reduced by the presence of the other. This result is, however, over-simplistic, since *O. ambulans* often increased its proportion in the culture (Fig. 2), due to differential mortality. *I. viridis* had a greater mortality rate than *O. ambulans*, and hence in mixed species cultures *O. ambulans* often dominated eventually.

Another factor to consider in such competition experiments is the fecundity of the competing species. Sparkes' data indicated that neither temperature nor the presence of *O. ambulans* significantly affected the fecundity of *I. viridis* (approxi-

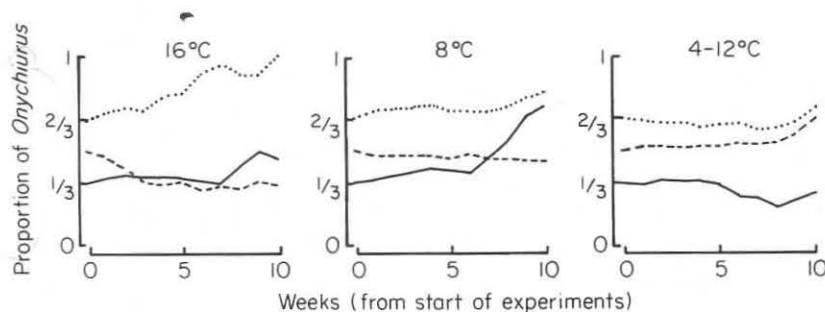


FIG. 2. The proportion of *Onychiurus ambulans* in mixed cultures with *Isotoma viridis*, over a 10-week period. The cultures were maintained in three temperatures, two constant (8° and 16°C) and one variable with a mean of 8°C but varying diurnally from 4°C to 12°C. Continuous lines represent cultures which started with 33% *O. ambulans*, dashed lines with 50% *O. ambulans*, and dotted lines with 67% *O. ambulans*. Data from Sparkes (1982).

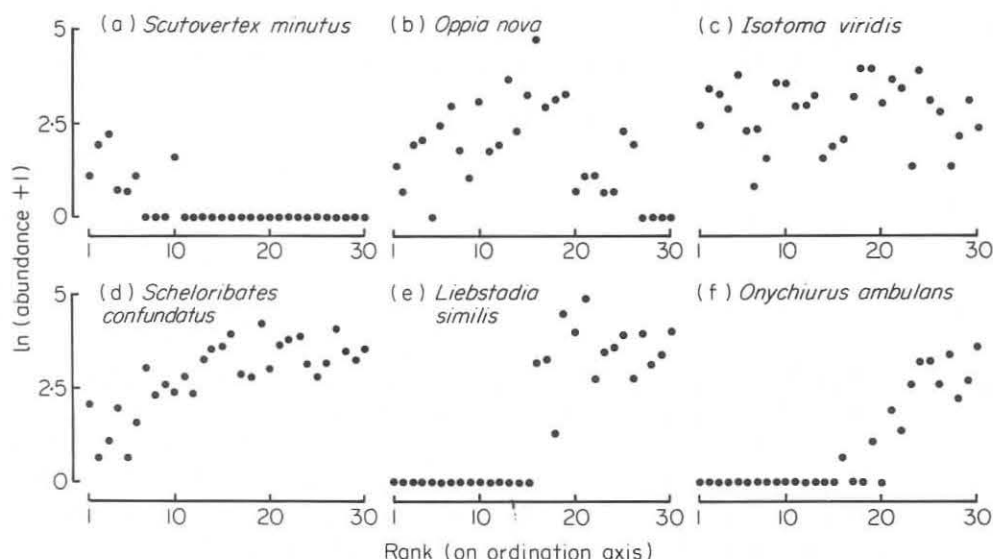


FIG. 3. The distribution of six arthropods (two Collembola, *I. viridis* and *O. ambulans*, and four Cryptostigmata) in relation to a successional gradient in Wharram Quarry Nature Reserve, Yorkshire. The successional ranking, based on a multivariate analysis as described in the text, runs from youngest (1) to oldest (30). Data from Parr (1980).

mately 0.7 eggs per female per day, assuming a 1:1 sex ratio). However, *O. ambulans* was strongly affected by both temperature and the presence of *I. viridis*: at 8°C a female laid approximately 3.7 eggs per day, whereas in the presence of *I. viridis* this rate dropped to 0.6 (again assuming a 1:1 sex ratio).

Laboratory studies of competition have tended to yield confusing results (e.g. Longstaff 1976). Few studies have demonstrated true competition, in which the fitness of both competing species is reduced, but many have indicated amensalism, whereby the fitness of only one competitor is reduced whilst that of the other is not altered significantly. Such asymmetrical competition (Lawton & Hassell 1981) is widespread in the insects. However, competition may not lead to the species with an unimpaired fitness 'winning': Fig. 2 demonstrates that *O. ambulans* often becomes proportionately more abundant in cultures, and Figs 3c and f also indicates that it slowly becomes dominant in the field (though competition in the field has not been investigated). The actual life-history attributes of the species, such as fecundity, mortality and speed of development from egg to reproductive adult, are as important in determining the outcome of competition as the actual interaction between the species.

Predation

There are essentially five questions to answer: what are the predators, how do they locate their prey, how do they catch their prey, how many do they eat, and what are the effects of predation on the prey population?

Beetles of the family Carabidae frequently predate Collembola, e.g. *Notiophilus* sp. (Higgins 1982) and *Loricera pilicornis* (Bauer 1982). Dennison & Hodkinson's (1983) study of a community of Carabid beetles showed that 17 out of 25 species in a woodland had been predating Collembola and 17, 13, 9, 8 and 3 had been predating mites, nematodes, spiders, enchytraeid worms and isopods, respectively. Spiders are probably important predators as well: it seems inconceivable that a population of *Notiomaso australis* in a moss-turf on South Georgia, with a density of approximately 1.5 cm^{-2} , was predating anything other than the abundant Collembola (Usher 1984). This species subsequently moulted and laid eggs when maintained in a laboratory on the Collembola, *Setocerura georgiana*. The Mesostigmata also contains many species of small predators, and some Collembola will eat animal material (Tosi 1977).

Studies have shown that many predatory mites appear to wander randomly when searching for prey (Davis 1978; Usher & Bowring 1984), although it is possible that there are chemical stimuli deriving from prey faeces (Hislop & Prokopy 1981). Relatively little is known about the mechanisms of capture, although studies of the chelicerae of Mesostigmata (Harris 1974; Karg 1983) indicated the type of prey, and Usher & Bowring (1984) found that some species use their forelegs for holding the prey whilst the chelicerae pierce the prey's side. When attacked, some Cryptostigmata are able to withdraw into a hardened cuticle (e.g. *Hoploverma* spp.), some Collembola are able to jump, and others may possess a chemical defence (e.g. pseudocelli function in *Onychiurus*: Usher & Balogun 1966; Rusek & Weyda 1981).

Rates of predation vary according to the species of prey, the degree of satiation of the predator, and the reproductive state of an adult mite. Harris & Usher (1978) showed that the form of the functional response of *Pergamasus longicornis* changed

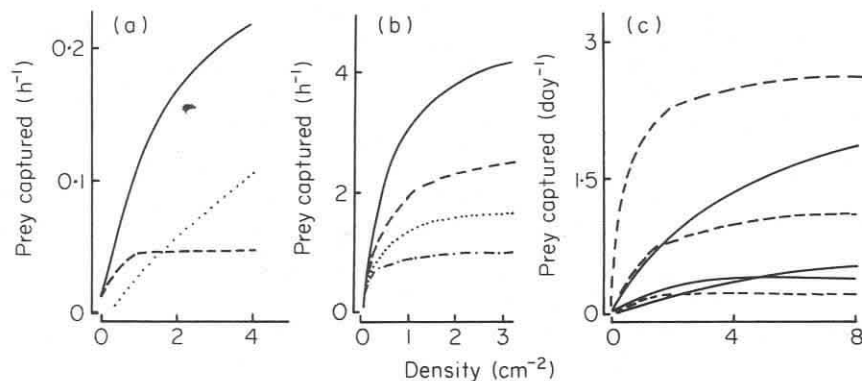


FIG. 4. Functional response curves for a variety of Mesostigmata predating Collembola in the laboratory. (a) male *Pergamasus longicornis* predating *Folsomia fimetaria* (—), *Sinella coeca* (....) and *Hypogastrura denticulata* (---). Data from Harris & Usher (1978). (b) male *Pergamasus crassipes* predating *Onychiurus armatus*. The four lines, from top to bottom, represent satiation of the predator (0–2 h, 2–4 h, 4–6 h and 6–8 h feeding respectively). Data from Longstaff (1980). (c) *Hypoaspis aculeifer* predating *Sinella coeca* (—) and *Hypogastrura denticulata* (---). The three lines (from top down) represent feeding on small, medium and large sized prey respectively. Data from Davis (1978).

from approximately a linear increase when the species was predating *Sinella coeca* to a very limited response when it was predating *Hypogastrura denticulata* (see Fig. 4a). Longstaff (1980), working with the closely related *Pergamasus crassipes*, found a similar type 2 functional response (Holling 1966), but the rate of predation decreased as the predators became satiated (Fig. 4b).

These results can be related to the possibility of predatory control of populations in the field. A type 2 functional response implies that, for all but the smallest prey populations, a doubling of prey density is not accompanied by a doubling of predation rate. This led Harris & Usher (1978) to suggest that predators were unlikely to exert a controlling influence on a species such as *H. denticulata*, which relies on chemical repulsion of the predator, but much more likely to be able to control a species such as *S. coeca*. However, Joosse (1981) has argued that the risk of predation is related to prey locomotion. The predation rate on *Tomocerus minor* by *Notiophilus biguttatus* was 26% in 8 days in dry environments, whereas in wet environments, where the prey moves less, the rate was 5% in 8 days. There is still much that is unknown about the effects of predators on the density of populations in the field.

Herbivory

The aim of this section is not to review the feeding of soil arthropods, but rather to concentrate on two questions: (i) what happens to fungi when they are grazed, and (ii) do the fungi have any defences against grazing animals? The review will concentrate on fungi rather than on bacteria since it is known that the majority of Cryptostigmata (Behan-Pelletier & Hill 1983) and Collembola (Petersen 1971; Takeda & Ichimura 1983) are fungal grazers. However, fungal grazing may not be particularly important in relation to the whole soil ecosystem: Mitchell & Parkinson (1976) estimated that only 2% of the fungal standing crop in an aspen woodland soil was consumed in one year by Cryptostigmatid mites.

Cancela da Fonseca, Kiffer & Poinso-Balaguer (1979) described the associations of mites and fungi that they detected in the forest soil, but what might be the reason for these associations? Four effects of grazing have been noted in the literature. First, grazing may contribute to the structuring of the fungal community. Parkinson, Visser & Whittaker (1979) have demonstrated how the competitive colonizing ability of two fungi can be altered by *Onychiurus subtenuis* grazing, although they were wary of extrapolating laboratory results to a field situation. Wicklow & Yocom (1982), however, felt that grazing by larval *Lycoriella mali* (Diptera: Sciaridae) in rabbit dung reduced the number of species of coprophilous fungi, and hence was important in structuring fungal communities. Second, grazing may affect the respiration of the fungi. Grazing by *Onychiurus armatus* on *Mortierella isabellina* (Bengtsson & Rundgren 1983) reduced respiration when grazing was continuous, but it increased respiration above that of an ungrazed culture when grazing was interrupted. Third, arthropods can distribute fungal spores in the soil, although many spores will be damaged and become non-viable with ingestion.

Behan & Will (1978) found that only 14% of faeces of seven Cryptostigmata species contained viable spores, and Ponge & Charpentier (1981) showed that spore viability decreased on passage through the gut of *Pseudosinella alba* (for *Penicillium* sp. it decreased from 69–100% to 3–11%). Fourth, it is possible that soil arthropods are associated with root pathogens, although Ulber (1983) has shown that infection of sugar-beet with *Pythium ultimum* is lower in the presence of Collembola.

Very little is known about how fungi can defend themselves against grazing. Wicklow (1979) has suggested a mechanical means whereby perithecial hairs protect the ascocarps of *Chaetomium bostrycodes*. The poisonous nature of many mycorrhizal fungi has led Shaw (p. 333) to speculate that the poisons may be anti-herbivore compounds, though *Drosophila* larvae are able to develop in the fruiting bodies of some of these poisonous species (Lacy 1984).

Three trophic levels

The majority of studies of the soil ecosystem have tended to infer relationships from field and from simple laboratory experiments. Some studies have used a wider spectrum of organisms: a producer (usually a higher plant), an associated microbe, and a grazing arthropod; or alternatively a microbe, its grazer and a predator of that grazer. Insufficient is yet known about the biology of soil organisms to know if there are 'top carnivores', and hence whether or not it would be possible to study the grazer–predator 1–predator 2 form of triple interaction.

There are a few studies of the higher plant–mycorrhiza–Collembola interaction (Warnock, Fitter & Usher 1982; Finlay 1983; Finlay, p. 319; Shaw, p. 333). Warnock *et al.* (1982) used a simple laboratory system of leeks, *Allium porrum*, infected with *Glomus fasciculatum*, and grazed by *Folsomia candida*. They found that infected plants in the presence of Collembola grew little better than uninfected plants, whilst infection in the absence of Collembola led to a significant increase in leek production and phosphate uptake. They argued that the Collembola grazed the external hyphae of this vesicular-arbuscular mycorrhiza. The presence of mycorrhizal infection also affected the populations of *F. candida*, which increased from an initial 20 per pot to an average of 53 in non-mycorrhizal treatments and to 140 in mycorrhizal treatments during a 12-week period. Analysis of gut contents indicated that the majority of Collembola with contents contained fungal material, although about 45% of the population had no visible gut contents. This figure is similar to that recorded by Anderson & Healey (1972), McMillan (1975) and Muraleedharan & Prabhoo (1978), the latter quoting ranges of 33–55%, 33–77% and 50–89% for three species of Collembola collected from the field in India. The former authors suggested that Collembola are only active for 50–60% of their adult life, whilst the latter authors attributed the lack of gut contents to a 'non-feeding phase of the inter-moult period'. What implications such a 'resting phase' may have for the population dynamics of Collembola remains unknown.

There are too few data to draw any general conclusions on such complex

interactions. Some studies have shown that mycorrhizal infection can be rendered virtually inoperative in the presence of grazers, whilst Ulber (1983) shows that lethal infections of sugar-beet with *Pythium* can be reduced from 100% to 22–75% in the presence of *Onychiurus* and to 9% in the presence of *Folsomia*. The introduction of a predatory mite into such systems is an experiment that has not yet been undertaken.

DYNAMICS OF NATURAL COMMUNITIES

Number of species and diversity

There has been some discussion as to whether or not the community of soil animals is unusually diverse: Anderson (1975) and Ghilarov (1977) have argued that it is, whilst Usher *et al.* (1979) have argued that it is possibly less diverse than communities above ground. The purpose of this review is to concentrate on some aspects of diversity that will be used subsequently.

Stanton (1979) looked at the communities in Wyoming and Costa Rica, sampling pine forests, broad-leaved forests and field communities in each country. The diversity of all four forest sites was similar (12–14 species of litter-inhabiting mites per 100 g litter) and greater than the field sites (5 species per 100 g of litter). Stanton plotted species–area curves for all six sites, indicating that the usual relationship between the number of species (S) and area (A),

$$S = CA^z$$

where C and z are constants, holds for the soil fauna as well as for many other organisms (see, for example, the review by Connor & McCoy 1979). The implications of this relationship seem not to have been realized by soil zoologists when writing about species richness, or species diversity, though the generality of the relationships for the soil fauna remains unknown.

Nine dominance–diversity curves for Collembola were shown by Usher *et al.* (1979): their sites were all of a climax or near climax nature, and the curves corresponded reasonably well with those produced by a log normal distribution (see Fig. 5a for the shapes of such curves under various assumptions about the distribution of individuals amongst species). Data for Collembola from a variety of ecosystems are shown in Fig. 5b. The two steepest curves relate to a moss-turf habitat on Signy Island (Usher & Booth 1984) and a *Deschampsia antarctica* sward on Lynch Island (Usher & Edwards 1984), both Antarctica, and they correspond to a steep, geometric series distribution. The shallower line relates to Sparkes' (1982) samples from a successional ecosystem in the Yorkshire Wolds: it also approximates to a geometric series distribution. Finally, two coniferous woodland curves, one from North Wales (Poole 1961) and the other from Caledonian pine forest in Scotland (Usher 1970), are shown. Such curves have been used in the interpretation of plant communities (Greig-Smith 1983): it would seem that similar use can be made for curves plotted using soil arthropod data.

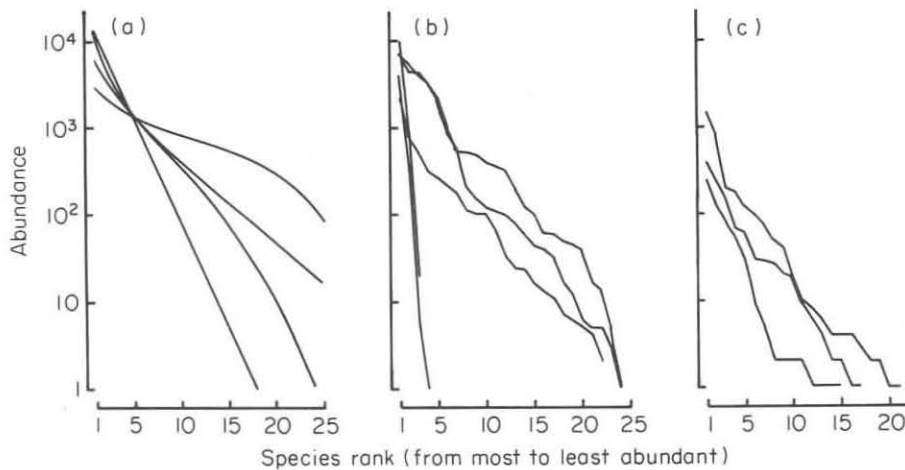


FIG. 5. Dominance-diversity curves for communities of Collembola. (a) Four theoretical distributions representing, from bottom to top at species rank 15, a geometric series, a log normal distribution, a logarithmic series, and MacArthur's distribution respectively. Drawn from a diagram in Whittaker (1972). (b) Data for five Collembolan communities, representing, from left to right at the 10^2 level, a Signy Island moss-turf, the Lynch Island grass sward, Wharram Quarry Nature Reserve, a Scots pine forest, and a mixed coniferous forest respectively. Sources of data are listed in the text. (c) Data for three successional communities of Moor House National Nature Reserve, representing, from left to right at the 10^2 level, the communities in *Eriophorum angustifolium*, *Eriophorum vaginatum* and *Calluna vulgaris*. Data from Hale (1963).

Relationship of species complement to site type

Gisin's (1943) pioneering work in Switzerland, relating faunal lists of Collembola to site types, led to numerous similar faunal studies, including other groups of the soil fauna, e.g. Rajski (1961) for Cryptostigmata in Poland and Huţu (1982) for Mesostigmata (Uropodidae) in north-eastern Romania. Other studies have attempted to relate arthropod communities directly to various environmental factors. Buxton (1981) related both the structure of a termite community, and its activity, to local variations in rainfall. Cotton & Curry (1982) looked at the distribution of earthworms along a gradient from mineral soil to peat, the peat having 75% of the species (compared with the mineral soil), 15% of the numbers, but only 9% of the biomass. Acidic pH and lack of suitable food apparently restricted the earthworm community at the peat end of the gradient. A principle components analysis to investigate the relationships between the environment and the mite and Collembola communities showed that the mites were related to soil organic matter content, moisture content, base status, but not to the site vegetation (Curry 1978). The Collembola community was related to neither the soil nor the vegetation. In another study (Curry & Ganley 1977) no relationship was shown between the presence of either mite or Collembola species and the roots of higher plants in an Irish pasture. In contrast Hågvar (1982) demonstrated a relationship between the Collembola communities and vegetation in a Norwegian coniferous forest. The

relationship became stronger as environmental conditions became more extreme, and this may explain why Curry's studies failed to demonstrate relationships in Irish lowland pastures.

There are three interacting factors of a site: the soil environment, the vegetation, and the community of soil animals. It is clear that little is yet understood about how strong the relationships are, or under what circumstances a relationship might or might not be expected. A study of ecosystems which are actively changing, either naturally or experimentally, may aid the unravelling of these relationships.

Changes in communities

Three categories of changes can occur in communities. First, there is the natural process of succession which, as primary or secondary succession, affects the whole community in which the soil animals live. This form of succession should be distinguished from the sequence of organisms associated with the decomposition of a dead organic product (Usher & Parr 1977) such as arthropods in an acorn (Winston 1956) or nematodes in cow dung (Sudhaus 1981). Second, changes follow an alteration in the management of the site (e.g. sheep grazing or forestry). Third, it is possible to alter communities deliberately as part of an experimental programme to investigate community structure. Such perturbation experiments are, unfortunately, rare.

Succession

There are relatively few descriptions of succession in animal communities. Huhta *et al.* (1979), who documented the fauna of some artificial soils made of crushed pine or spruce bark and sewage sludge, noted that the first colonists were flying insects, phoretic mites and nematodes, arriving within a few days. Collembola arrived after a few weeks, and the Cryptostigmata arrived later still. Succession of Collembola in agricultural soil (Hermosilla 1982) was accompanied by an increase in diversity over a 494-day period, though an increase is virtually inevitable when one starts from nothing or nearly nothing. Two further examples of succession can be investigated in detail. One relates to the cyclical process of peat build-up in heather moorlands and its subsequent erosion, and the other relates to a primary succession on the floor of an abandoned chalk quarry.

Hale (1963, 1966) and Block (1965, 1966) described the Collembola and mites respectively of moorland in northern England. The position of *Eriophorum vaginatum* in the successional sequence (Table 3) is that adopted by Hale (1963). In general, the number of species and the number of individuals of Cryptostigmata, Prostigmata and Collembola increased during the successional sequence, but the density of Mesostigmata reached an upper limit more speedily. Whelan (1978) similarly showed a rapid increase in the number of Mesostigmata colonizing peat, but this is in contrast to the colonization of colliery spoil (Hutson & Luff 1978).

TABLE 3. Arthropods associated with the succession on eroded peat at Moor House National Nature Reserve. The successional sequence of the vegetation is shown, together with the numbers of species (*S*) and density in thousands per m² (*N*). The data are taken from Hale (1963) and Block (1966)

Vegetation type	Collembola		Mesostigmata		Other Acari	
	<i>S</i>	<i>N</i>	<i>S</i>	<i>N</i>	<i>S</i>	<i>N</i>
Bare peat*	2	0	0	0	2	0
<i>Eriophorum angustifolium</i>	17	4.7	—	0.6	—	25.4
<i>Eriophorum vaginatum</i>	14	24.4	—	4.1	—	29.9
Mixed moor	26	31.0	20	3.2	45	45.5
Hummock top	25	38.8	—	2.5	—	95.0

* No permanent populations of mites or Collembola on bare peat.

where the predatory Mesostigmata were slow to colonize the new habitats. Dominance-diversity curves for the stages of the moorland succession (Fig. 5c), however, show little change in shape.

In the chalk quarry (Parr 1980), no distinct stages in the ecological succession had been determined quantitatively *a priori*. Parr ordinated the arthropod data for the thirty areas that he sampled: the horizontal axes in Figs 3 and 6 are the first ordination axis which was identified as representing the successional sequence. Figure 3 demonstrates that the species complement changes with succession: density also increases with successional age (Fig. 6). The number of species of mites increased during the succession, but that of Collembola remained virtually constant. A measure of diversity, the Brillouin Index *H*, also increased during succession, although in the Collembola there was an indication that *H* decreased in the centre of the range due to the dominance of a few species.

Parr (1980) had only a small segment of a full successional sequence, but, like Hale (1963), he demonstrated that the total community tended to increase in abundance, species richness and diversity, although there may be periods of relative constancy in one or more of these measures of the community structure.

Management

The effects of silvicultural practices in Finland on the soil fauna (e.g. Huhta *et al.* 1967; Huhta 1976), of manuring increasing populations but reducing diversity (Weil & Kroontje 1979), of ploughing having only short-term effects (Loring, Snider & Robertson 1981), and of organic farming increasing both species richness and abundance of carabid beetles (Dritschilo & Erwin 1982), have all been described. The effects of management can be demonstrated by the Collembola in six pastures in New South Wales, Australia: pairs of pastures had sheep stocking intensities of 10, 20 and 30 sheep ha⁻¹ (King, Hutchinson & Greenslade 1976). The most noticeable effect of the increased stocking was on the overall abundance of Collembola, which decreased from 117 100 m⁻² to 63 200 m⁻² to 5100 m⁻² respectively. The number of species was also reduced, but by a smaller factor, decreasing from 21 to 17 to 15 respectively. The changes in diversity were not so clear cut, although there was some evidence that it increased slightly with increased stocking.

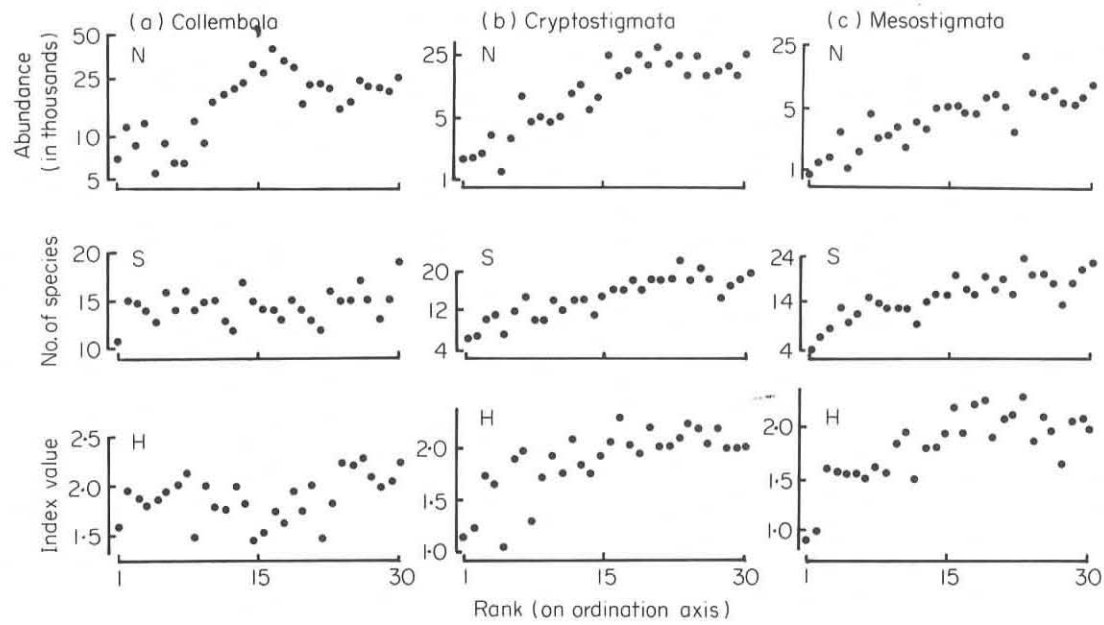


FIG 6. Changes in the number of individuals (N), number of species (S) and the Brillouin Index (H) of the Collembola, Cryptostigmata and Mesostigmata during the succession in Wharram Quarry Nature Reserve. The successional rank (1 = youngest, 30 = oldest) is used in Fig. 3 and described in the text. Data from Parr (1980).

Of the 28 species recorded on the pastures, 15 species were found in pastures of all stocking intensities, and a further 9 were in the lightly and intermediately stocked pastures. Two rare species were not found in the least stocked pastures, and two other rare species were found on the most and least intensively stocked pastures. The evidence suggested that species were lost from the pastures as the stocking intensity increased.

To understand the results of management one should consider both changes in quantities of food for the soil fauna, and structural changes in the soil habitat. Manuring and organic farming resulted in increased arthropod populations, and clear felling of forests (Huhta 1976) led to a temporary (about one decade) increase in Lumbricid and Enchytraeid worm populations: all these increases could be attributed to extra organic matter. On the other hand trampling (Garay & Nataf 1982), compaction or drastic disturbance destroyed the soil habitat, decreasing populations of soil animals.

Perturbation

The dividing line between management and perturbation experiments is small: perturbation experiments are, however, designed specifically to investigate interactions. The design of a series of replicated experiments was discussed by Usher, Booth & Sparkes (1982), but results of these experiments are not yet available. An experiment in a Canadian spruce forest with nitrogen (as urea) resulted in very minor changes in the species composition, density, and vertical distribution of soil arthropods (Behan, Hill & Kevan 1978). The comparisons were between untreated and treated (nitrogen at 220 kg ha^{-1}) plots, but whether the small changes are general or due to resilience of the old spruce forest remains unknown. Insecticides have frequently been used; for example, application of DDT to cultivated forest soil in Nigeria resulted in a decrease of Mesostigmata ($10\,260$ to 590 m^{-2}) and an increase in Collembola (9060 to $35\,310 \text{ m}^{-2}$; Perfect *et al.* 1981), but whether the latter is coincidental or the result of release from predation is unknown. A study in a Swedish pine forest by Bååth *et al.* (1980) showed that acidification of a soil resulted in a decrease in Mesostigmata (6180 to 2900 m^{-2}) and an increase in Collembola ($33\,270$ to $48\,270 \text{ m}^{-2}$). The study investigated many aspects of soil biology, and showed that acidification also decreased populations of Enchytraeids and of some species of Cryptostigmata, and radically changed the community of bacteria.

Such perturbation experiments, designed to investigate the concurrent changes in the populations of many species in the soil, and suitably replicated, provide an experimental tool that soil biologists have hardly started to use. This kind of experimentation is likely to be a profitable field for future research.

DISCUSSION

To conclude this review there is one aspect of the population dynamics of soil

organisms that should be discussed. This is concerned with the links between the decomposer food web and the more general theories of population dynamics in ecology. To what extent are the general theories applicable to the decomposer ecosystem, and what might a study of decomposers contribute more widely in ecology?

It is true that the majority of aspects of population dynamics—fecundity, mortality, movement into or out of populations—and of interactions between populations—competition, predation, herbivory—are essentially the same in any food web, be it above- or below-ground, and hence general theoretical developments can be applied to any of the systems. There are, however, three possible differences when the soil arthropod communities of temperate latitudes are considered. One of these differences concerns a diapause, and whether hatching is synchronous or staggered over a long period of time leading to pulses of juveniles entering a population. A second difference concerns the ability of the soil fauna to function throughout the year: the soil environment is buffered from climatic extremes, the temperature at a depth of 25 cm being recorded as not dropping below 2°C during the British winter (Frazer 1983). Third, there has been some discussion as to whether the soil fauna show features of *r*- or *K*-selection (Gerson & Chet 1981), but a more interesting concept is that of *A*-selection (Greenslade & Greenslade 1983). *Adversity-selection* would be shown in species in communities of continuously harsh, and hence predictable, environments, and it is postulated that diversity is low and there are few interactions between species in such communities. The concept of *A*-selection is thus very similar to that of stress-tolerance in plant ecology (see Grime 1979). Greenslade & Greenslade (1983) suggest that one should look for *A*-strategists in Australia on mountain tops, in cold wet forests, in the arid zone, and deep in the soil. The first three habitats are places where the majority of the local fauna actually live in the soil, and it is perhaps the soil fauna that have adopted a form of *A*-strategy more than any other fauna. Certainly the data for the two Antarctic sites (Fig. 5b) represent communities from extremely harsh environments, and would probably represent communities of *A*-strategists: can one postulate that the individuals in such communities would have log series distributions amongst the species?

The soil ecosystem tends to be one that has been forgotten by ecologists, perhaps because soil unlike water or air is opaque and perhaps because there are few attractive species (colourful, cuddly, or cute) that live within it. However, there are a number of interesting aspects of the population and community dynamics that have been discovered, and probably many more to be discovered, especially where interactions between more than two trophic levels are considered. It has the one great advantage for researchers that it exists, and is experimentable with, for 12 months of each year in all but the most extreme climates.

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